PSYCHE

Vol. 86 March, 1979 No. 1

THE PHENOLOGY OF *PIERIS NAPI MICROSTRIATA* (LEPIDOPTERA: PIERIDAE) DURING AND AFTER THE 1975–77 CALIFORNIA DROUGHT, AND ITS EVOLUTIONARY SIGNIFICANCE*

By Arthur M. Shapiro
Department of Zoology,
University of California,
Davis, California 95616, U.S.A.

Introduction

Interest in the theoretical basis of insect phenology has increased very markedly in recent years (Bradshaw, 1974; Cohen, 1970; Giesel, 1976; Levins, 1969). The evolution of phenological "strategies" via natural selection is of interest to ecologists and applied entomologists alike. Insect phenology involves responses to both "normal" and "abnormal" weather. The developmental plasticity displayed by a population may determine its survival in seasons of unusual meteorological stress and in turn may reflect a history of selection by recurrent exposure to that stress.

The 1975–77 California drought was a short-term climatic anomaly with no equal in the meteorological records of that state. Any event of such magnitude would be expected to affect both phenology and reproductive success of a great variety of organisms, especially annual or ephemeral species. Since 1972 the phenology of entire butterfly faunas has been monitored along a transect paralleling Interstate Highway 80 from sea level at Suisun Bay to 2750 m at Castle Peak, north-central California. This has permitted year-to-year comparisons within localities as well as within-year comparisons among localities. This long-term study involving over 150 species includes the 1975–77 drought and the tremendous rains of winter 1977/78. Certain butterfly populations showed very pro-

**Manuscript received by the editor June 30, 1979.*

nounced fluctuations during this period. One of the most dramatic, and one whose behavior can be rationalized at a mechanistic (proximate) level, is *Pieris napi microstriata* Comstock.

Seasonality of *P. n. microstriata*

The *Pieris napi* (L.) complex, which probably includes several genetic species, is circumpolar in distribution and largely restricted to cool-temperate to subarctic climates. In California about four subspecies occur, only two of which are well-known biologically: *P. n. venosa* Scudder, confined to the coastal fog belt, and *P. n. microstriata* which occurs farther east in the Inner Coast Ranges and on the west slope of the Sierra Nevada. These populations, now disjunct, were probably connected in riparian forest in the Central Valley as recently as the mid-19th century (Shapiro, 1978). *P. n. venosa* is normally double- to partially triple-brooded, with two seasonal phenotypes (Shapiro, 1975, 1977) under photoperiod and temperature control. *P. n. microstriata* is normally univoltine, with only a spring phenotype (Shapiro, 1975, 1976a, 1977). It is capable of producing a summer phenotype and may have a partial second brood in some localities in some years. This most often occurs in Coast Range localities subject to occasional maritime influence, as around the Napa Valley.

Populations of *P. n. microstriata* occur at two of the regular sampling stations along I-80: Gates Canyon, an east-facing canyon on the east slope of the Vaca Hills (Inner Coast Range) near Vacaville, Solano Co. (50–600 m), and Lang Crossing of the South Yuba River in the mixed-conifer belt of the Sierran west slope, Nevada Co. (1350–1500 m). These are matched with nearby U.S. Weather Bureau stations of record at Vacaville and Blue Canyon Airport, respectively. Some aspects of the host-plant relations of the butterflies are described in Shapiro, 1974 and 1976b. Both populations fluctuated during the most anomalous year (1977), but in opposite directions. Both were quantified by direct census of both adults and immatures.

Gates Canyon

The history of this population since 1972 is given in Table 1. The 1972 estimate is unreliable because only one sampling day is involved, but all of the others are based on weekly to biweekly visits through the flight season.

The California drought began with the failure of the 1975 autumn rains. The 1975 flight of *P. n. microstriata* was rather poor, and both adult and immature numbers were down. Spring 1976 started warm (January +1.1°C compared to Vacaville means), turned cooler in April, then very warm (+1.9°) in May. The flight of *P. n. microstriata* was the largest ever observed at Gates and lasted for three months, although only one generation was involved. The sex-ratio was normal (about 1.7:1) and over 200 eggs and 50 larvae were seen. The host plants, *Barbarea verna* (Mill.) Asch. and *Dentaria californica* Nutt. (both Cruciferae) were early, of somewhat better than average luxuriance, and senesced early with the onset of hot weather in May–June. There was nothing meteorologically unusual about the months when 1975 eggs and larvae were developing, which would have promoted unusual survival. The very large adult population in 1976 could be due to diminished mortality due to predators, parasites, and disease or to direct meteorological effects on the dormant pupae.

Winter 1976/77 was the second grossly deficient rainfall season. January–March 1977 were statistically unremarkable for temperature. The adult population of *P. n. microstriata* was almost non-existent, despite the great burst of reproduction the previous year. Four males were seen—one each on four days—and at least one

Table 1. Populations of *Pieris napi microstriata* at study sites.

Year	*Inclusive dates of flight season*	*N (rounded up to nearest 5 from census)*
	(a) Gates Canyon, Solano County, California	
1972	iii.28 (only visit)	—
1973	iii.23–iv.18	30
1974	iii.13–v.19	50
1975	iv.9–v.2	25
1976	ii.21–v.2	75+
1977	iii.10–iv.28	5
1978	iii.14–v.7	30
	and (2nd brood) v.20–v.28	5
	(b) Lang Crossing, Nevada County, California	
1974	v.5–vi.2	20
1975	v.18–vi.9	30
1976	not studied	
1977	iv.17–v.13	50
1978	v.3–vi.9	20

female must have flown because a single egg was found 11 April. It must have failed to develop since there was no damage at all to the plant on the 28th. The biomass of *Barbarea* was reduced by roughly an order of magnitude relative to 1976, and the number of plants decreased very markedly. This facilitated search for early stages, and host plant coverage was especially good in 1977. It is thus uncertain that any successful reproduction by *P. n. microstriata* took place in Gates Canyon this year.

Winter 1977/78 brought record heavy rainfalls (Table 2). Rather than being extinct, as would be expected for an obligate annual, *P. n. microstriata* was back at pre-drought numbers. Most of the emergence was early: females were already present on 14 March and eggs were found on the less-preferred host *Dentaria* (*Barbarea* was late). By 9 April there were eggs, small larvae, and large larvae on most of the *Barbarea* plants and some on *Dentaria.* One male each was seen on 21 April and 7 May (none on 29 April). By 7 May only a handful of large larvae remained. On 20 and 28 May single males of the rare second generation (*castoria* phenotype)—the first ever recorded in the Vaca Hills—were found.

Simultaneously, the Pierid *Anthocaris sara* Lucas, which is also facultatively bivoltine, produced an abundant second generation which flew from 20 May–21 June, as in southern California coastal localities (Emmel and Emmel, 1973). The Hesperiid *Erynnis propertius* (Scudder & Burgess) and the Lycaenid *Incisalia iroides* (Boisduval) also produced second broods which flew to 21 June and 2 July respectively.

Lang Crossing

Here there are no 1976 data, and the irregular topography makes coverage of potential hosts less accurate. However, the 1977 events make a striking counterpoint to those in Gates Canyon (Table 1).

The 1976/77 winter produced very little snow at mid-elevations. Although it was a mild winter, cumulative chilling experienced by diapausing pupae near ground level was undoubtedly enhanced by lack of snow cover. Lang Crossing was completely snow-free on 17 April and 20 species were flying, including male *P. n. microstriata.* By 22 April females were flying and laying on *Barbarea* and on *Nasturtium officinale* R. Br. April temperature was below normal but the weather was fair until the very end of the month, after most

Table 2. Precipitation at nearest weather stations to study sites.

Water year (July 1–June 30)	Vacaville rainfall, cm	Blue Canyon Airport total precip., cm	Blue Canyon Airport snowfall, cm
1971–72	26.19	133.48	676.15
1972–73	88.67	180.28	743.46
1973–74	66.35	244.43	769.62
1974–75	55.73	175.06	743.20
1975–76	23.47	88.27	302.26
1976–77	23.32	68.53	225.55
1977–78	95.78	223.19	751.84

of the egg-laying had been completed. Cold rains then began and turned to snow: on 5 May, 15 cm of snow fell; by 8 May this had increased to 33 cm. There were daily rain showers thereafter until 18 May. On 13 May, with north-facing slopes snow-covered, as many plants as were exposed were censused. 43 eggs and 2 small larvae were found on *Barbarea*. On 21 May the same plants, along with others and several *Arabis glabra* (L.) Bernh., were again censused but not one egg or larva was found. Larval feeding damage was limited to the pinholes inflicted by first-instar larvae. Insofar as could be determined, the entire 1977 reproductive output was lost. Other than a soft-winged female found 13 May, no more adults were seen.

Harcourt (1966) found that rain was a major mortality factor for eggs and larvae of *Pieris rapae* (L.) on cabbage in Canada.

Winter 1977/78 saw a return of heavy snowfall, but there was also so much warm rain that snow packs were not good, and Lang was snow-free 12 April: 10 species, not including *P. n. microstriata*, were flying. 32 cm of snow fell 15 April, with cold rain 24–25 and 28 April. On 3 May one male was seen. Snow fell again 23–24 May. On 29 May and 2 June *P. n. microstriata* were common, with eggs on the latter date on (in descending order of preference), *Arabis*, *Nasturtium*, and *Barbarea*. The last adult seen was 9 June; on 15 June 3 mature larvae were still found on *Arabis*.

Discussion

There is little in the literature on catastrophic extinctions of natural butterfly populations (Ehrlich *et al.*, 1972). Both populations of *P. n. microstriata* under study flirted with extinction in 1977, for different reasons. As an early spring insect, *P. n. microstriata* trades off lateness of emergence (to reduce the probability of catastrophic weather-induced mortality) against earliness (to match the phenology of the vernal Crucifers). The former factor would seem more compelling at Lang, the latter at Gates. How do *P. n. microstriata* "decide" when to emerge?

Under controlled laboratory conditions populations show an astonishing intrapopulational variance in the "chilling requirement" to break pupal diapause. There seem to be interpopulational differences as well, but for the purposes of Table 3 pupae from four

Table 3. "Chilling requirement" to break diapause in *P. n. microstriata*. Dormant pupae were held at 3° C and tested at intervals at 20° to ascertain whether diapause had been broken. Pooled data for several broods (see notes), 1972 through 1978.

	Genetic diapausers[1]		*Facultative diapausers*[2]	
Number of weeks[3] *held at 3° prior to activation*	*Number of pupae activating*	*Percent of all pupae*	*Number of pupae activating*	*Percent of all pupae*
5–9	12	2.9	0	0
10–14	14	1.0	9	9.2
15–19	9	2.2	30	30.6
20–24	11	2.7	24	24.5
25–29	49	12.1	13	13.3
30–34	78	19.3	8	8.2
35–39	111	27.4	5	5.1
40–44	37	9.1	1	1.0
45–49	41	10.1	1	1.0
50–54	15	3.7	0	0
55–59	3	0.7	0	0
60–64	7	1.7	0	0
65–69	3	0.7	1	1.0
70–74	8	2.0	0	0
75–79	4	1.0	0	0
greater than 79	13	3.2	6	6.1

notes:

[1]defined as individuals which diapaused under continuous light at 20° C+. From 14 females ex 3 foothill populations and 1 mid-elevation Sierran population.

[2]defined as individuals which diapaused under inducing photoperiods at 20° C+. Since these broods included some genetic diapausers which would have diapaused anyway, these are included in the tally. From 4 females ex 2 foothill populations.

[3]time elapsed does not include pre-testing time and testing time to assess dormancy at 20°.

populations are pooled. There is a difference between genetic "obligate" diapausers, which are refractory to photoperiod, and facultative diapausers which have been reared on inducing regimes, as well as a large spread of developmental times in each group. How this variability is expressed afield is unclear. Except for some pupae which do not develop at all in the first year, all individuals probably come out of diapause in January and subsequent development is temperature-dependent. The accumulated chilling in continuous cold storage is much greater than the wild pupae experience in fluctuating temperatures, so the "chilling requirement" is really a more complex chilling-time interaction. Except for pupae which carry over to a second or subsequent year, the effect of intrapopulational variance may be largely masked in cold, wet springs and maximally expressed in warm, dry ones.

The carryover pupae provide the only reasonable explanation for the large 1978 population at Gates after the 1977 disaster. The numbers, however, suggest that a large number of carryover pupae may have been involved. This in turn suggests that something about the 1976/77 season cued a carryover response in a larger-than-usual fraction of the population. The temperature pattern is conveniently similar to 1977/78; the striking difference is rainfall.

Carryover pupae occur in other Pierids, including *Anthocaris sara* and *A. cethura* (Felder & Felder), *A. lanceolata* Lucas, *Euchloe hyantis* (Edw.), *E. ausonides* Lucas, and *Pieris sisymbrii* Bdv. in western North America. They also occur in *Papilio rudkini* Comstock (Papilionidae), a desert swallowtail noted for its aseasonality, correlation of flights with heavy rains, and diapause pupae which may carry over for 6 years or more (Emmel and Emmel, 1973 and *pers. comm.*). There is strong circumstantial evidence for this species that a physiological response to water initiates post-diapause development—the insect behaves like a desert annual plant with a water-soluble seed-germination inhibitor. Of the Pierid species listed above, some occur in xeric and some in more mesic habitats, but not enough data are available to say whether the frequency of carryover pupae is correlated with rainfall uncertainty in the habitat.

In any case, *P. n. microstriata* is a surprising insect to have the carryover response, given that it is almost certainly of Arcto-Tertiary mesic origin (Shapiro, 1975, 1977). Years of 25 cm or less of rain have occurred 14 times at Sacramento since 1849 and 14 times at Davis, Yolo County, since 1871. For both only the 1975/76 and 76/77 water years stand as consecutive severe doughts. At both stations 1930/31 and 32/33 were dry, separated by an average year, and at Davis 1917/18 and 1919/20 were dry, separated by a wet year. Is the long-run rainfall variance in central California adequate to select for a carryover response, or is it a preadaptive property of Pierids generally? Data on populations from other climates are needed.

It is dangerous to argue that because an aspect of the biology of an animal is adaptive in a particular situation, it evolved as a response to that situation in evolutionary time. In the case of *P. n. microstriata* at Gates it is not clear that a tenfold reduction in host biomass would have adversely affected fitness, had the insect attempted to reproduce. (Compare Murdoch, 1966 for a Carabid beetle case.) We simply do not know if intra- or interspecific competition for food would have occurred. Because *P. n. microstriata* is usually out of phase with *Dentaria* at Gates, it uses that plant mainly at the beginning of the flight and in early years, and most of its eggs are placed on the phenologically better-matched *Barbarea,* even though *Dentaria* is more abundant. Its eggs are strongly contagiously distributed, and it does not assess egg load on individual hosts, so that single plants sited such that females find them easily may receive overloads of eggs. It can thus be argued that with fewer and smaller plants intraspecific competition would have been aggravated—but we do not know if oviposition behavior might have been modified. *P. n. microstriata* is also positively associated with *A. sara* on individual hosts. This butterfly seems to assess its own egg load but not that of *P. n. microstriata.* The *Pieris* is a leaf-, the *Anthocaris* a silique-feeder. In 1977 there was no conspicuous reduction in numbers of *A. sara* adults or eggs at Gates, even though it is able to carry over (indeed, most captive pupae do); its 1978 performance was outstanding. A major reduction in host biomass, then, failed to adversely affect it, perhaps because it distributes eggs more evenly.

We do not know where the 1978 butterflies at Lang came from. Some may have been carryovers, but here the destruction of the 1977 egg crop may have been more apparent than real. Many hosts at Lang are inaccessible for censusing, and precisely these—on steep, wooded slopes—may have afforded more benign microclimates to eggs and larvae than those at and near canyon bottoms. In most years 75–80% of potential hosts are censused at Gates, but only 50% at Lang.

There are two major modeling approaches to insect phenology. One, the physiological-time or degree-day approach, began with Shelford's (1927) study of the codling moth, *Laspeyresia pomonella* (L.) (Tortricidae). This is still the best-quantitated species (Riedl, Croft and Howitt 1976; Riedl and Croft, 1978). Here the emphasis is on the development of predictive algorithms from empirical data. The other approach proceeds from Darwinian principles and is exemplified by the treatment of Levins (1969) or Cohen (1970) who derive strategies from survival and reproduction parameters. The two approaches are complementary: responses to real meteorological events are the proximate consequences of selection for a genetic blueprint of development. The fusion of the two approaches into a comprehensive theory of insect phenology will require data on how seasonality contributes to resource utilization, competition, and survival.

Acknowledgements

Field assistance in 1977 was provided by Susan J. Katz. This research was funded in part by grant D-804 from the Committee on Research, U.C. Davis.

Literature Cited

Bradshaw, W.E. 1974. Phenology and seasonal modeling in insects. *in* H. Lieth, ed., *Phenology and Seasonality Modeling*. Springer, New York. pp. 127–138.

Cohen, D. 1970. A theoretical model for the optimal timing of diapause. *Amer. Nat. 104:* 389–400.

Ehrlich, P. *et al.* 1972. Weather and the "regulation" of subalpine populations. *Ecology 53:* 243–247.

Emmel, T. C. and J.F. Emmel. 1973. *The Butterflies of Southern California*. Los Angeles County Museum of Natural History.

Figgins, W. E. 1971. Climate of Sacramento, California. *NOAA Tech. Mem. NWS-WR65*. 63 pp.

Giesel, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Ann. Rev. Ecol. Syst. 7:* 57–79.

Harcourt, D. G. 1966. Major factors in survival of the immature stages of *Pieris rapae* L. *Can. Ent. 98:* 653–662.

Levins, R. 1969. Dormancy as an adaptive strategy. *Symp. Soc. Exptl. Biol. 23:* 1–10.

Murdoch, W. W. 1966. Aspects of the population dynamics of some marsh Carabidae. *J. Anim. Ecol. 35:* 127–156.

Riedl, H. and B. A. Croft. 1978. The effects of photoperiod and effective temperatures on the seasonal phenology of the codling moth (Lepidoptera: Tortricidae). *Can. Ent. 110:* 455–470.

Riedl, H., B. A. Croft, and A. J. Howitt. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological time models. *Can. Ent. 108:* 449–460.

Shapiro, A. M. 1974. Host-plant utilization by *Pieris napi* populations in California. *Psyche 81:* 361–366.

______. 1975. Developmental and phenotypic responses to photoperiod in uni- and bivoltine *Pieris napi* in California. *Trans. R. Ent. Soc. London 127:* 65–71.

______. 1976a. Photoperiodic responses of phenologically aberrant populations of Pierid butterflies. *Great Basin Nat. 35:* 310–316.

______. 1976b. The role of watercress, *Nasturtium officinale,* as a host of native and introduced Pierid butterflies in California. *J. Res. lepid. 14:* 158–168.

______. 1977. Phenotypic induction in *Pieris napi* L.: role of temperature and photoperiod in a coastal Californian population. *Ecol. Ent. 2:* 217–224.

______. 1978. Photoperiod and temperature in phenotype determination of Pacific Slope Pierini: biosystematic implications. *J. Res. Lepid. 16:* 193–200.

Shelford, V. E. 1927. An experimental investigation of the relations of the codling moth to weather and climate. *Ill. Nat. Hist. Survey Bull. 16,* number 5.

U.S. Department of Commerce. Environmental Data Service 1971–77. Annual climatological summary, Vacaville, CA.

______. 1977. Annual summary with comparative data. Blue Canyon, CA.